TARDIGRADES OF THE AUSTRALIAN ANTARCTIC TERRITORIES: ASSESSING DIVERSITY WITHIN A SAMPLE

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Miller, W.R., Miller, J.D. & Heatwole, H.F. 1994 06 30: Tardigrades of the Australian Antarctic Territories: assessing diversity within a sample. *Memoirs of the Queensland Museum* **36**(1): 137-145. Brisbane. ISSN 0079-8835.

A 10 × 10 × 5cm sample was collected from a moss bed near Casey Station in the Australian Antarctic Territory and analysed as a series of 27 subsamples, which were reassembled in layers and columns to examine the distribution of tardigrades in the original sample. Three genera containing four species of tardigrades were recovered from the subsamples: *Diphascon chilenense*, *Pseudechiniscus suillus*, *Hypsibius antarcticus* and *D. pinguis*. Tardigrades were not evenly distributed horizontally or vertically; nor did a strong association occur among the species. The results indicate that although small diameter core samples minimise damage to fragile moss beds in harsh climatic areas such as the Antarctic, single samples do not necessarily provide an accurate assessment of the distribution or diversity present.
Australia, Antarctic, biodiversity, Tardigrada, sampling, ecology, taxonomy.

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The terrestrial ecosystems of continental East Antarctica are confined to small areas of unfrozen coast and to nunataks that protrude through the ice (Holdgate, 1967). These 'islands' (sensu Miller et al., 1988), situated in a sea of mostly frozen water, exhibit a rudimentary soil that is inhabited by bacteria, yeasts, fungi, unicellular algae, rotifers, nematodes, tardigrades and mites (Heatwole, 1983; Heatwole et al., 1989). A few species of lichens and mosses grow on this soil and the surrounding rocks (Lamb, 1970); as the primary flora, the lichens and mosses harbour an assortment of microscopic plants and animals.

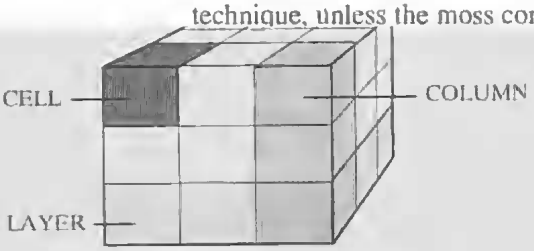
Because of the extreme conditions under which Antarctic mosses grow (Greene & Longton, 1970; Lamb, 1970), they form micro-environmental units that can be destroyed by disruption (Opalinski, 1972). As a result of very slow growth rates (Longton & MacIver, 1974), recovery following disruption or sampling might require years (Seppelt & Ashton, 1978) even in less extreme climates such as southern Australia (Scott & Stone, 1976). Obviously, minimal sampling is required to prevent destruction of the moss bed. However, a conflict occurs between the need to not disrupt the internal environmental conditions required for growth, and the need to sample enough of the moss to provide a representative collection of the micro-organisms that inhabit it.

The qualitative method used for sampling micro-fauna inhabiting moss beds is commonly called a 'grab' sample because the dimensions are not defined or are only poorly defined. This type of sampling has been used in broad-based surveys and/or systematic studies and has commonly included multiple samples taken from relatively small areas (e.g. Riggin, 1962; Morgan & King, 1976; Nelson & Horning, 1979; Horning et al., 1978; Dastych, 1984). Although 'grab' samples may be useful in the context of a survey to assess the number of species present, without multiple samples the assessment may be an underestimate. Because they are of unknown size and volume, 'grab' samples can not be used to estimate population size, density, biomass (Jennings, 1976a) or distribution within the sample.

The use of small diameter or square core samples (e.g. Hallas, 1975; Jennings, 1976a; Miller et al., 1988; Miller et al., 1994) seems to satisfy the need to obtain regular quantitative samples; however, the use of only a few cores to assess the species diversity in a moss turf carries with it the assumption that the core sample is representative of the microfauna and flora inhabiting the larger floral unit. The use of pooled cores, 3 or more small diameter cores, taken a few centimetres apart and combined to form a composite sample has been used (Jennings, 1976a) to satisfy some of the statistical requirements of representing the larger environment. Contiguous square samples (2 × 2 × 0.5cm) have been used to assess the distribution of tardigrades in relation to the micro-environment of the moss turf (Hallas, 1975). Although coring is a very useful sampling

FIG. 1. Location map showing the relative positions of Australia and Casey Station.

technique, unless the moss cores are subdivided



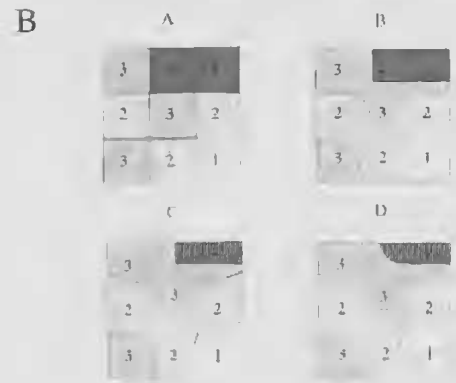


FIG. 2. A. Terminology used for describing parts of the 10×10×5cm sample of Antarctic moss. B. Illustration of the process of smoothing used in constructing the distributional patterns of four species of tardigrades inhabiting the volumetric sample of Antarctic moss. Top face of sample is illustrated; numbers indicate the number of species in each column (see text for details).

zero during the middle of the day but regularly drop below freezing at night. The average temperature in December is 2.2°C (Bureau of Meteorology, 1988).

METHODS

Field work was done during the austral summer program of the Australian National Antarctic Research Expeditions (ANARE) in December 1982. The sample analysed here was collected as a part of a general survey of the study area (Miller et al. unpub data).

A single 10 cm square was cut from the moss bed to the depth of the underlying substrate (approximately 5 cm). The resulting sample was removed and immediately divided into three layers (each approximately 1.6cm thick); each layer was subdivided into nine small cells (approximately 3.3×3.3×1.6cm). Each cell was dried in an individual paper bag at room temperature. The process of preparation of the specimens

A

into two or more layers, the vertical distribution of tardigrade numbers or species in the sample can not be addressed.

The purpose of the present study was to determine the distributional patterns of tardigrade numbers and species within a single volumetric sample of Antarctic moss. The sample was analysed according to the hypotheses of (1) uniform distribution for numbers of tardigrades, (2) even diversity of species, and (3) equal association among the species.

STUDY AREA

The sample was taken from an unsheltered site below a melt-water lake near the new Casey Station (66°17'S, 110°32'E) on the Bailey Peninsula in Wilkes Land, East Antarctica (Fig. 1). The ocean side of the area (Vincennes Bay) is dotted with the low, rocky Windmill islands. To the east is the Loken Moraine, which marks the limit of the exposed rock. To the north is the Clark Peninsula where the abandoned Wilkes Base is located. To the immediate south of Casey Station is the Mitchell Peninsula; further south is Browning Peninsula and the Vanderford Glacier. Throughout the area, patches of seasonally exposed rock are separated by permanent ice fields. A few exposed areas exceed two hectares in size; however, most are much smaller. In the summer, air temperatures may rise several degrees above

and slides was described by Miller et al. (1988). The distribution of tardigrades within the total sample was determined by combining the results obtained from analysis of individual cells into layers and columns (Fig. 2A). Assessment of species diversity was based on the presence or absence of a species in each of the cells; determination of the inter-specific association among the species was based on the expected joint occurrence of each pair of species. Statistical analysis followed Zar (1984) and Miller et al. (1994).

A three-dimensional model based on the number of species found in each cell was constructed to represent the distribution of the tardigrade species within the total sample (Fig. 2B). The initial construction of the model assumed that the cells were discrete units containing specific numbers of tardigrade species. The boundaries between cells were smoothed to form polygons representing the potential patterns of distribution of the species based on two assumptions: (1) that a cell with a large number of species would contain areas occupied by fewer species (i.e. assuming an uneven distribution of species within the cell) and (2) that a cell with a low number of species could not contain an area occupied by a higher number of species. After a distributional pattern was developed for each face of the sample, the model was drawn in 3-D perspective.

RESULTS

At the time of collection, the moss turf was on a well drained gravel/stone substrate. The moss was green in the upper portion of the first layer only; the lower portion of the first layer and the two lower layers appeared brown. There was more plant litter in the bottom layer than in the two upper layers.

The only moss species found in the sample was *Bryum argentium* Hedwig, 1801, a moss that grows in densely tufted cushions. *B. argentium* has reddish-brown stems that are matted with simple radicles, erect leaves that are oblong and concave, and yellow-green to green leaves that are reddish at the base. The nerve of the leaf is well defined and reddish-brown in colour; under magnification the cells of the leaf are an irregular rhomboid-hexagonal shape. *B. argentium* is known from Syowa (Tatuno, 1963), the Vestfold Hills (Seppelt, 1984), Casey Base (Seppelt & Selkirk, 1984) and is considered a cosmopolitan moss (Longton, 1981).

Three genera containing four species of tardigrades were represented in the 1568 specimens recovered from the total sample. A taxonomic account of these is given in Dastych (1984). They are listed below in order of relative abundance in the total sample:

	Diphascon chilenense	*Pseudechiniscus suillus*	*Hypsibius antarcticus*	*Diphascon pinguis*	TOTAL (Percent)
I	740 (47.2)	43 (2.7)	31 (2.0)	5 (0.3)	819 (52.2)
LAYER II (Percent)	540 (34.4)	9 (0.6)	2 (0.1)	0 (0)	551 (35.1)
III	198 (12.6)	0 (0.0)	0 (0.0)	0 (0.0)	198 (12.6)
TOTAL (Percent)	1478 (94.3)	52 (3.3)	33 (2.1)	5 (0.3)	1568 (100.0)

FIG. 3. Distribution by layer of four species of tardigrades recovered from a 10 × 10 × 5cm sample of Antarctic moss.

Diphascon chilenense langhovdensis (Sudzuki, 1964); 1478 specimens or 94.3%.

Pseudechiniscus suillus (Ehrenberg, 1853); 52 specimens (3.3%).

Hypsibius antarcticus (Richters, 1904): 33 specimens (2.1%).

Diphascon pinguis (Marcus, 1936); 5 specimens (0.3%). *D. pinguis* is known from King George Island (Dastych, 1984), South Shetland Island and South Georgia (Jennings, 1976a, b), but not before from East Antarctica.

All 27 cells of the sample contained at least one species of tardigrade (*D. chilenense*), 8 cells (29.6%) contained two species (*D. chilenense*, and *P. suillus*), 3 cells (11.1%) contained three species (*D. chilenense*, *P. suillus* and *H. antarcticus*) and 2 cells (7.4%) contained all four species (Table 1). Two or more species were represented in 48.1% of the cells and three or more occurred in 18%. The actual number of animals (regardless of species) in a cell ranged from 0 to 158 (Table 1). There was a significant departure from the hypothesis of even distribution (χ^2 [$p_{0.05}$= 38.89, 26]= 923.37), indicating that the tardigrades did not occur uniformly among the cells of the moss sample. When considered separately, the distribution of *D. chilenense*, which occurred in all cells, was not even (χ^2 [$p_{0.05}$= 38.89, 26]= 888.28) among the cells.

When the cells were combined to form the three layers of the original sample (Fig. 3), 819 of the 1568 specimens (52.2%) were recovered from the top layer, 551 (35.1%) from the second layer, and

TABLE 1. Distribution of tardigrade species by cell from a 10×10×5 cm sample of Antarctic moss.

Diphascon chilenense

	Column									
Layer	1	2	3	4	5	6	7	8	9	Total
I	73	135	46	50	64	65	114	158	35	740
II	24	39	42	141	41	47	125	67	14	540
III	10	24	40	42	36	9	8	12	17	198
Total	107	198	128	233	141	121	247	237	66	1478

Pseudechiniscus suillus

	Column									
Layer	1	2	3	4	5	6	7	8	9	Total
I	3	3	1	2	5	13	11	5	0	43
II	3	2	1	3	0	0	0	0	0	9
III	0	0	0	0	0	0	0	0	0	0
Total	6	5	2	5	5	13	11	5	0	52

Hypsibius antarcticus

	Column									
Layer	1	2	3	4	5	6	7	8	9	Total
I	2	2	26	0	1	0	0	0	0	31
II	0	1	0	0	0	0	1	0	0	2
III	0	0	0	0	0	0	0	0	0	0
Total	2	3	26	0	1	0	1	0	0	33

Diphascon pinguis

	Column									
Layer	1	2	3	4	5	6	7	8	9	Total
I	0	3	2	0	0	0	0	0	0	5
II	0	0	0	0	0	0	0	0	0	0
III	0	0	0	0	0	0	0	0	0	0
Total	0	3	2	0	0	0	0	0	0	5

198 (12.7%) from the bottom layer. *D. chilenense* was found in all layers in contrast to *D. pinguis*, which was found only in the top layer; the other two species, *H. antarcticus* & *P. suillus*, were found in layers I and II but not in layer III. Based on the total number of tardigrades in each layer, there was a significant departure from the hypothesis of even distribution among the layers (χ^2 {$p_{0.05}$= 5.99, 2}= 371.2), indicating that tardigrades did not occur uniformly among the layers. Although *D. chilenense* was found in all three layers, its distribution was not even (χ^2 {$p_{0.05}$= 5.99, 2}= 292.6) among the layers.

When the cells were combined to form nine vertical columns (Table 2), *D. chilenense* was found in all columns; *P. suillus* was recovered from 8 columns. *H. antarcticus* occurred in 5 columns and *D. pinguis* was collected from only 2 columns. Based on the total number of tardigrades in each column, there was a significant departure from the hypothesis of even distribution among the columns (χ^2 {$p_{0.05}$= 15.51, 8}= 200.34), indicating that the tardigrades did not occur uniformly among the columns. The distribution of *D. chilenense*, the only species found in all columns, was uneven (χ^2 {$p_{0.05}$= 15.51, 8}= 204.12) among the columns.

In terms of assessing species diversity and distribution of tardigrades within a moss bed, the subsampling of the 10×10×5cm sample

TABLE 2. Distribution of tardigrades in columns of a 10×10×5 cm sample of Antarctic moss. In each box, number in square identifies column; large number indicates the number of species; small numbers indicate the number of individuals from each species. Percentage is based on the total for each column and the total number (1568) of tardigrades.

											Species
1	107	2	198	3	128	*Diphascon chilenense*
	6		5		2	*Pseudechiniscus suillus*
	2		3		26	*Hypsibius antarcticus*
	0		3		2	*Diphascon pinguis*
3	115	4	209	4	158	Total
Species	7.3%	Species	13.3%	Species	10.1%	Percent
4	233	5	141	6	121	*Diphascon chilenense*
	5		5		13	*Pseudechiniscus suillus*
	0		3		0	*Hypsibius antarcticus*
	0		0		0	*Diphascon pinguis*
2	238	3	147	2	134	Total
Species	15.2%	Species	9.4%	Species	8.6%	Percent
7	247	8	237	9	66	*Diphascon chilenense*
	11		5		0	*Pseudechiniscus suillus*
	3		0		0	*Hypsibius antarcticus*
	0		0		0	*Diphascon pinguis*
3	259	2	242	1	66	Total
Species	16.5%	Species	15.4%	Species	4.2%	Percent

provides instructive results. Assuming that a subsample would be taken from only one of the nine columns (Fig. 2, Table 2), only two (22.2%) of the 9 columns that could be sampled would have contained all 4 species; another three (33.3%) would have contained three species. Of the remaining four columns, three (33.3%) would have yielded only two of the four species present in the total sample and the last (11.1%) would have revealed only one. There was an 88.8% chance that a single column taken from the total would not contain all four species that actually inhabited the sample.

The greatest number of species did not occur in the columns with the greatest number of specimens (Table 2). Three contiguous columns (4, 7, 8) (Table 2) contained (47.1%) of all specimens recovered; however none of these contained all four species. Both columns 2 and 3 contained four species but only 23.5% of the total number of specimens combined (13.4%, 10.1%, respectively). Columns in which three species occurred ranged from a low of 7.3% of the total number of individuals to a high of 16.5%. Three columns, each containing 2 species, yielded 8.6%, 15.5% and 15.2% percent of the total, respectively. The column that contained only one species did contain the fewest individuals.

When the three layers and nine columns were considered together (Fig. 3, Table 1, 2), there was a clear vertical trend of decreasing numbers of *D. chilenense* with depth into the moss sample. In 7 of the nine columns, layer I contained more specimens than layer II; in 2 columns, layer II contained the most *D. chilenense*. In 8 of the 9 columns, layer II contained more specimens than layer III. In one column, layer III contained more *D. chilenense* than layer II but only by 3 individuals.

Fifty-two *Pseudechiniscus suillus* were recovered from 12 cells (44.4%) from 8 columns of the total sample. Most specimens (43) were recovered from layer I; the remaining 9 were recovered from layer II. None were found in the bottom layer.

The total sample contained 33 specimens of *Hypsibius antarcticus* in 6 cells (11.2%). Most (31) were recovered from layer I; the remaining 2 were recovered from layer II. None were found in layer III. All except 2 specimens occurred in columns 1, 2 and 3.

Five *Diphascon pinguis* were found in 2 cells (7.4%) of contiguous columns (2, 3); all were found in layer I.

Within the 10×10×5cm sample, the four species occurred together in only 2 columns (Table 2). The three species (*D. chilenense*, *P. suillus* & *H. antarcticus*) occurred together in 3 columns; the two species (*D. chilenense* & *P. suillus*) occurred together in 3 columns. One species (*D. chilenense*) occurred alone in one

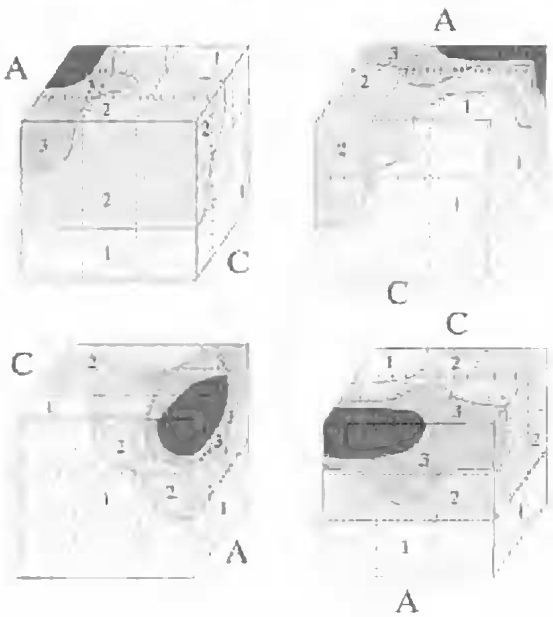


FIG. 4. Three dimensional model representing the distribution of four species tardigrades in a 10×10×5cm sample of Antarctic moss.

TABLE 3. Inter-specific association based on the expected pattern of joint occurrence within cells between pairs of tardigrade species recovered from a 10 × 10 × 5cm sample of Antarctic moss.

	LAYERS			COLUMNS			CELLS		
Species × Species	P=0.05 expected	χ^2=5.99 observed	df=2 χ^2	P=0.05 expected	χ^2=15.51 observed	df=8 χ^2	P=0.05 expected	χ^2=38.89 observed	df=26 χ^2
D. chilenense × *P. suillus*	2.00	2.00	0	8.00	8.00	0	12.00	12.00	0
D. chilenense × *H. antarcticus*	2.00	2.00	0	5.00	5.00	0	6.00	6.00	0
D. chilenense × *D. pinguis*	1.00	1.00	0	2.00	2.00	0	2.00	2.00	0
P. suillus × *H. antarticus*	2.00	2.00	0	3.56	4.00	0.90	2.67	5.00	4.73
P. suillus × *D. pinguis*	0.67	1.00	0.75	1.78	2.00	0.32	0.89	2.00	2.70
H. antarcticus × *D. pinguis*	0.67	1.00	0.75	1.11	2.00	2.06	0.44	2.00	7.56

column. The least common species, *D. pinguis*, occurred only in the columns with the greatest diversity of species; it never was found alone or just with other infrequently occurring species.

However, χ^2 analysis for inter-specific association between species-pairs of tardigrades exhibited no great departure from the expected numbers of joint occurrences based on the numbers of the species within the cells and established that the tardigrades were not highly associated or disassociated (Table 3).

The smoothing of the boundaries between contiguous cells based on the number of species present in each and the rotation of the 3 dimensional model allow inferences to be made concerning the distribution of the species within the sample (Fig. 4). There was an increasing gradient from the bottom to the top of the sample and from one side to the other. The irregularly shaped pattern of distribution of the species extends beyond the boundaries of the sample and is probably controlled by factors outside the sample. The analysis of inter-specific association among the tardigrades suggests that they probably respond more to variations in the micro-environment of the sample than to each other. The complexity of the distribution of the tardigrades can be demonstrated by comparing the pattern shown in Fig. 2B to that depicted in Fig. 4. Three species are recorded in the lower left corner of Fig. 2B (which represents the total for column 7) but not in column 7 of the 3-D model (Fig. 4) because the three species do not occur together in any one cell of the column.

DISCUSSION

Many species of Antarctic tardigrades are widely distributed (McInnes, 1994); others have restricted distributions (Miller et al., 1988; Dastych, 1984, 1989). For example, the distribution of *Pseudechiniscus suillus* is relatively well known; it has been reported from the Antarctic as well as at least 8 separate land-masses and oceanic islands. In contrast, the distributions of *Diphascon chilenense* and *Hypsibius antarcticus* are incompletely known; this probably reflects the distribution of collecting effort more than the actual distribution of the species. A good example of the process of range extension is the expansion of the known distribution of *Diphascon pinguis* to include Casey Station in East Antarctica. Without doubt, as more collections are analysed further extensions in range will occur.

At the level of the collection site, tardigrades are known to be unevenly distributed through the habitat and do not necessarily occur in every sample (e.g. Hallas, 1975, 1977; Schuster & Grigarick, 1970; Miller et al., 1988). Reconstruction analysis of the distribution of tardigrades within the 10 × 10 × 5cm sample confirms the previous observations and indicates that the tardigrades were not uniformly distributed among the layers. The tardigrades were concentrated in the uppermost layers of the sample, probably in response to the same environmental conditions of the Antarctic summer that effect the moss, including moisture, temperature and light (Greene & Longton, 1970; Lamb, 1970; Seppelt & Ashton, 1984). Moisture may be the most important factor influencing the distribution of the tardigrades in the sample (Hallas, 1975); but the presence of food may also be an influence.

After analysing 66 contiguous 2 × 2cm square samples that were between 0.5 and 0.8cm thick, Hallas (1975) pooled the species to view the

distribution of the numbers of tardigrades because one species represented 91% of the 368 specimens recovered. His results (Hallas, 1975: fig 2) show an uneven distribution of 1-13 individuals per square that is very similar to the pattern shown in Table 2 (i.e. greater numbers of individuals in some areas and fewer in other areas). The concentration (based on biomass) of the tardigrades in the uppermost portion of the moss cushion where most of the moisture was situated (Hallas, 1975) is reflected in the highest numbers being found in the upper layer of the 10×10×5 cm sample (Table 1).

While neither the number of animals nor the number of species was evenly distributed within the total sample, the species occurred independently of each other (i.e. one species did not occur more frequently with another than would be expected). Yet, each species seems to be more concentrated in one area of the total sample (Table 1). *D. chilenense* is concentrated in columns 4, 7 and 8 while *D. pinguis* is concentrated in columns 2 and 3 as is *H. antarcticus*. *P. suillus* exhibits a broader, uneven distribution with some concentration in columns 6 and 7 of the sample. It is interesting to note that the greatest number of species did not occur in the columns or cells that contained the greatest number of specimens.

The skewed pattern of distribution of the tardigrade species toward the upper layer and to one side of the sample suggests that there may be unsampled areas of the moss turf where a fifth species may exist. Conversely, the paucity in both numbers and species of tardigrades in the opposite corner of the total sample suggests that some unsampled parts of the moss turf may be unoccupied by tardigrades.

Qualitative 'grab' samples may provide a measure of diversity but should be avoided because the undefined size of the sample precludes rigorous comparison with other samples and because any structure or pattern of distribution of the micro-fauna within the sample is lost. In contrast, small diameter core samples can provide quantitative information not only on the species composition, but also on relative abundance and patterns of association. For example, Jennings (1976a, b) used 3.5cm diameter (by 3.0cm depth) cores, where possible, to create a volumetric measure on which to base his population-density and bio-mass estimates. Most of the core samples were analysed in total; some were pooled to create bulk samples from which aliquots were drawn for analysis. Unfortunately, 'information on the spatial dispersion of the population is lost' (Jennings, 1976a) using these techniques. It should be noted that Jennings was concerned with differences in population structure and species richness between sites and not within sample distribution.

Hallas (1975) noted that obtaining information on the vertical distribution of species would be 'advantageous' to understanding the ecology of tardigrades. Information on the vertical distribution can be obtained by dividing cores into at least two (upper & lower) subsamples and is necessary to understand the patterns of association of the species inhabiting the sample. For example, analysis of column 7 without dividing it into layers yielded 3 species but when the distribution within the column was considered, two species (*D. chilenense* and *P. suillus*) occurred in the top layer, and a different combination of species (*D. chilenense* and *H. antarcticus*) occurred in the middle layer, and only one species (*D. chilenense*) occupied the bottom layer. This sort of result may eventually lead to an understanding of the distribution, patterns of association and response to environmental conditions.

Unless numerous cores are taken, the use of small diameter cores may not adequately sample the diversity of species within the moss turf. In the present study, there was only a 2 in 9 chance of collecting all four tardigrade species from the 10×10×5cm sample using the columns as cores. Clearly, if too sparse of a sampling pattern were imposed on the uneven distribution of tardigrade species in a moss turf, the result would be an underestimation of the species richness. However, the use of multiple cores to obtain samples from even a small area, increases the probability of accurately determining the species richness in the moss turf and of identifying real differences between areas. For example, using multiple cores to sample moss turfs on Signy Island, Jennings (1976a) found 16 tardigrade species at 43 sites but only 9 (21%) of those sites yielded more than 3 species. Likewise, he found 11 species at 70 sites on the Antarctic Peninsula and Scotia Ridge region, but only 7 (10%) had more than 3 species (Jennings, 1976b). These results approximate the results of analysing one or two columns of the 10×10×5cm sample without dividing them into layers. Obviously, the collection of multiple small diameter core samples from moss beds is necessary to accurately sample the diversity of the tardigrade inhabitants.

Based on the analysis of this 10×10×5cm sample, tardigrade distribution within an Antarctic moss sample is complex with both num-

bers and species being unevenly distributed horizontally and vertically. The analysis also illustrates the need to base the collection of moss samples on good sampling design to allow statistical analysis of the results. Multiple small diameter cores should be used to assess the microfauna inhabiting moss beds; the sampling practice should also ensure only minimal damage occurs to the moss turf.

ACKNOWLEDGMENTS

We are grateful to the Australian National Antarctic Research Expeditions (ANARE) and to the personnel of the Australian Antarctic Division, especially those at Casey Station. Other logistical support was financed by the Ian Potter Foundation and by Internal Research Grants from the University of New England, Armidale, N.S.W. Dr H. Dastych, University of Hamburg kindly confirmed the identifications of the tardigardes.

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